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Plates xii and xiii.

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Observations on the nervous control of the heart in decapod crustaceans were published in 1880 by Plateau,* who worked upon *Macrura* and *Brachyura*, obtaining substantially the same results in both. His conclusions were that accelerator impulses reach the heart from the cerebral ganglion over the so-called "cardiac nerve," while inhibitory impulses have their centre in the ventral chain of ganglia and can not be aroused by stimulation of the cerebral ganglion. The course of the fibres from the central nervous system to the heart was not followed anatomically, but Plateau believed that the "cardiac nerve" arose from the cerebral ganglion and passed backward along the under side of the ophthalmic artery to the heart, while he supposed the inhibitory nerve to accompany the sternal artery into the pericardium. These observations and conclusions, so far as the *Brachyura* are concerned, have been directly contradicted by the recent work of Jolyet and Viallanes on the European crab, *Carcinus mœnas*.† They found no trace of the existence of the "cardiac nerve," and they located both inhibitory and accelerator centres in the anterior part of the thoracic ganglion. One of their most important results was the discovery on each lateral wall of the peri-

* F. Plateau. Recherches physiologiques sur le cœur des Crustacés décapodes, *Arch. de biolog., vol. I.*

† F. Jolyet et H. Viallanes. Recherches physiologiques sur le système nerveux accélérateur et modérateur du cœur chez le crabe, *Ann. des sci. nat. zool.*, t. xiv, 1893.

cardium of a "ganglionic swelling" from which proceeded several nerves, evidently connected in some way with the action of the accelerator and inhibitory centres in the thoracic ganglion; but they did not trace out this supposed connection either anatomically or physiologically. As a supplement to their work, we undertook, at the suggestion of Professor Howell, a series of experiments on the American edible crab, *Callinectes hastatus*, which may be obtained in the markets of Baltimore throughout the greater part of the year. It may be said at once that so far as there are any disagreements between the work of Plateau and that of Jolyet and Viallanes, our observations have uniformly supported the latter. We have been unable to find any evidence of the existence of the so-called "cardiac nerve," and stimulation of the cerebral ganglion always gave reflex inhibition, which disappeared when the œsophageal commissures were cut. (Fig. 1, Plate XII.)

For a better understanding of the following experiments a brief description of the nervous system will first be given. As in all the *Brachyura*, the ventral ganglia in *Callinectes* are concentrated into the so-called thoracic ganglion, through the centre of which passes the sternal artery. The relation of the chief nerves to this ganglion will be readily seen in Fig. 7, Plate XIII. Attention is especially called to one pair (R C.) arising on the dorsal surface just behind its anterior edge. These pass obliquely upward to the lining of the carapace and the roof of the gill chamber, and are known as the "recurrent cutaneous" nerves. Posterior to these there arise on each side three small nerves, which pass upward and backward to a plexus within the pericardium on the same side. This plexus corresponds to the "ganglionic swelling" and its nerves, figured by Jolyet and Viallanes, and will be spoken of in this paper as the pericardial plexus. Of these three nerves, the most anterior (Fig. 7, Plate XIII, *a*), leaving the ganglion with the recurrent cutaneous nerve, runs upward close beside it for a short distance, and then, turning abruptly, passes backward along the side of the body cavity to the pericardial plexus. The middle nerve (Fig. 7, Plate XIII, *b*) leaves the ganglion near the base of the nerve to the third maxilliped and, passing out-

ward and upward, runs close beside the nerve just described, entering the plexus parallel to it. The third or posterior nerve (Fig. 7, Plate XIII, *c*) leaves the ganglion near the base of the first ambulatory nerve and, passing upward through a lobe of the liver, turns backward along the side of the body cavity and enters the plexus ventral and almost at right angles to the other two. The course and function of these three nerves were not worked out by Jolyet and Viallanes on *Carcinus*. While they figure all three entering the "ganglionic swelling," they make special mention only of the third, and of that they simply say that, passing into the substance of the liver, it loses itself in the direction of the thoracic ganglion.

In our work two methods of exposing the heart and nervous system were employed according to the experiment to be performed. Ordinarily the thoracic ganglion was laid bare by a large opening on the ventral side of the crab, as figured by Jolyet and Viallanes, while on the dorsal surface a portion of the carapace was removed just over the heart, the beat being thus recorded through the intact pericardium. The crab was then tied to a vertical frame so that the ventral surface was presented for stimulation, while the pericardium could be connected with the recording apparatus. This connection was made by a horizontal piece of pith to a delicate vertical tambour, which communicated by a rubber tube with a similar tambour placed horizontally. Upon the latter a pith upright transmitted the movements to a horizontal writing lever, which recorded upon a vertical drum.

In the second method, after exposing the nervous system as above, the heart was laid bare by cutting away everything on the ventral side down to the pericardium. The records were taken with the crab on its back by means of an upright resting on the heart and communicating directly with a horizontal writing lever.

It must not be supposed from the experiments given below that the response of the thoracic ganglion to electrical stimulation was always the same. Some crabs would give no acceleration until the inhibitory nerves were cut; others would give no inhibition so long as the accelerators were intact; with others, in poor condition, it was impossible to get either acceleration or inhibition satisfactorily.

Jolyet and Viallanes believed that the nerves *c* (Fig. 7, Plate XIII) carried both accelerator and inhibitory fibres, and they apparently supposed that the nerves *a* and *b* played no part in the nervous control of the heart. That such is not the case in *Callinectes* can be readily shown by cutting the nerves *c* at the plexus, after which acceleration and inhibition may still be obtained from the thoracic ganglion, while after cutting the nerves *a* inhibition can not be obtained from any point, even though the nerves *c* are intact. The following evidence is offered for the existence of separate inhibitory and accelerator nerves in *Callinectes*.

The Inhibitory Nerves.

Experiment I: showing the function of the nerves *a*.

Crab opened by the second method. Inhibition obtained by stimulation of the thoracic ganglion. The nerve *a* on each side cut inside the pericardium; no more inhibition from ganglion. The end of nerve *a* attached to plexus stimulated; prompt inhibition. (Fig. 2, Plate XII.)

Experiment II: showing physiologically that the nerves *a* enter the ganglion along with the recurrent cutaneous nerves.

Crab opened by the first method. All the nerves to the ganglion except the recurrent cutaneous cut, and inhibition still obtained from ganglion. Recurrent cutaneous nerves cut, and inhibition no longer obtained from ganglion, but produced at once on stimulation of the peripheral end of either recurrent cutaneous. (Fig. 3, Plate XII.)

Experiment III: showing that the nerves *a* are the only inhibitory nerves.

Crab opened by the first method. Inhibition obtained from ganglion. Recurrent cutaneous nerves cut. No further inhibition from ganglion, though all the other nerves were intact. Inhibition from peripheral end of recurrent cutaneous nerve, as in Experiment II.

Experiment IV: showing that the nerves *c*, which Jolyet and Viallanes believed to contain both the inhibitory and accelerator fibres, do not contain inhibitory fibres.

1. Crab opened by second method. Inhibition from ganglion. Nerves *c* cut inside the pericardium, and inhibition still obtained from ganglion. Nerves *a* cut inside the pericardium, and no further inhibition obtained except from stimulation of their peripheral ends.

2. (Converse of 1, on another crab.) Inhibition from ganglion. Both nerves *a* cut inside pericardium, and no further inhibition obtained except from their peripheral ends.

Cutting the inhibitory nerves (*a*) seems to have no effect on the heart beat except sometimes a very brief inhibition due to their stimulation; not the slightest evidence of their tonic activity was found.

The Accelerator Nerves.

Experiment V: showing the function of the nerves *c*.

Crab opened by the second method. Acceleration obtained from ganglion. Nerves *b* cut inside the pericardium; acceleration still obtained. Nerves *c* cut; no more acceleration from ganglion. Immediate acceleration from stimulation of the end of nerve *c* connected with the plexus. (Fig. 4, Plate XIII.)

Experiment VI: showing the function of nerves *b*.

Crab opened by the second method. Nerves *c* cut; acceleration still obtained from ganglion. Nerves *b* cut; no further acceleration from ganglion. Immediate acceleration from stimulation of the end of *b* connected with the plexus. (Fig. 5, Plate XIII.)

Experiment VII: showing that nerve *c* leaves the ganglion in the region of the first ambulatory nerve.

1. That *some* accelerator leaves at this place.

Crab opened by first method. All the nerves cut away from the ganglion except the first ambulatories; acceleration obtained from the ganglion. The first ambulatories cut; no more acceleration from ganglion.

2. That it is the nerve *c*.

Crab opened by second method. First ambulatory nerve on one side cut close to the ganglion and peripheral end stimulated; acceleration obtained. Nerve *c* on same side cut within the pericardium; no more acceleration obtained from peripheral end of first ambulatory nerve. Evidently nerve *c* was cut with the first ambulatory and remained attached to it.

Experiment VIII: showing that nerve *b* leaves the ganglion in the region of the third maxilliped nerve.

1. That *some* accelerator leaves at this place.

Crab opened by first method. First ambulatory nerves cut, the cut being made deeply to insure sectioning nerve *c*; acceleration still obtained from ganglion. Third maxilliped nerves cut deeply; no more acceleration from ganglion.

2. That it is the nerve *b*.

Crab opened by second method. First ambulatory nerves cut deeply; acceleration obtained from ganglion. Nerves *b* cut inside pericardium; no more acceleration from ganglion.

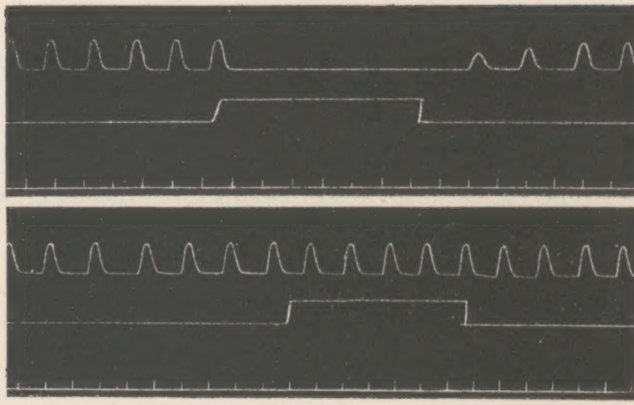
A very conclusive demonstration of the accelerator function of nerve *b*, as well as of the inhibitory function of nerve *a*, may be obtained by placing a pair of fine electrodes between the two nerves, and pressing upon first one and then the other. The marked acceleration given by *b* is followed immediately by inhibition on touching *a*, and *vice versa*.

That each of these three nerves to the heart leaves the ganglion as an independent nerve is shown by both anatomical and physio-

logical evidence. The accelerators (*b* and *c*) are much too delicate as they leave the ganglion to be seen in the living crab. In alcoholic material, however, they can be traced with the aid of a dissecting microscope and are found to preserve their independent course throughout. In the diagram (Fig. 7, Plate XIII) they are exaggerated in size, except at the plexus. Here they may be easily seen with the naked eye. The inhibitory nerves are larger, and by careful search can be seen in the living crab, running as separate fibres alongside the recurrent cutaneous nerves as they enter the ganglion. With the exercise of sufficient care the recurrent cutaneous, third maxilliped, and first ambulatory nerves can be cut without injuring the small nerves to the heart which accompany them. Ordinarily, however, cutting the first ambulatory nerves severs the one pair of accelerator nerves, and sometimes the other also, so that acceleration from the ganglion is no longer possible. In such cases stimulation of the peripheral end of the cut ambulatory gives acceleration usually (Fig. 6, Plate XIII), while stimulation of the process of the endoskeleton that lies just in front of the first ambulatory nerve on each side, about one centimetre from the ganglion, gives acceleration always. Both accelerator nerves pass over this process, and applying the electrodes to it evidently stimulates them.

As in the case of the inhibitory nerves, we found no evidence of tonic activity in either accelerator. In fact, the thoracic ganglion may be removed in part or in whole without apparently producing any effect on the rate of the heart beat. Evidently *Callinectes* differs from *Carcinus* in this respect, or else our material, not coming directly from the water, was less sensitive. It is worthy of remark that acceleration, as well as inhibition, is produced without any appreciable latent period, as examination of the figures will show.

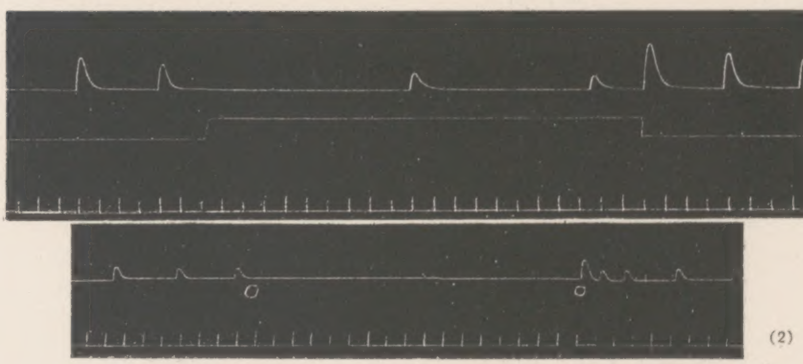
Jolyet and Viallanes state that cutting the fibres of the plexus between the two branchio-cardiac orifices renders impossible all inhibition or acceleration, and they therefore conclude that it is the posterior branches that carry the inhibitory and accelerator fibres from the plexus to the heart. In *Callinectes* we have cut the plexus as far forward as the anterior orifice, and found no evidence of



(1)

(2)

Fig. I.



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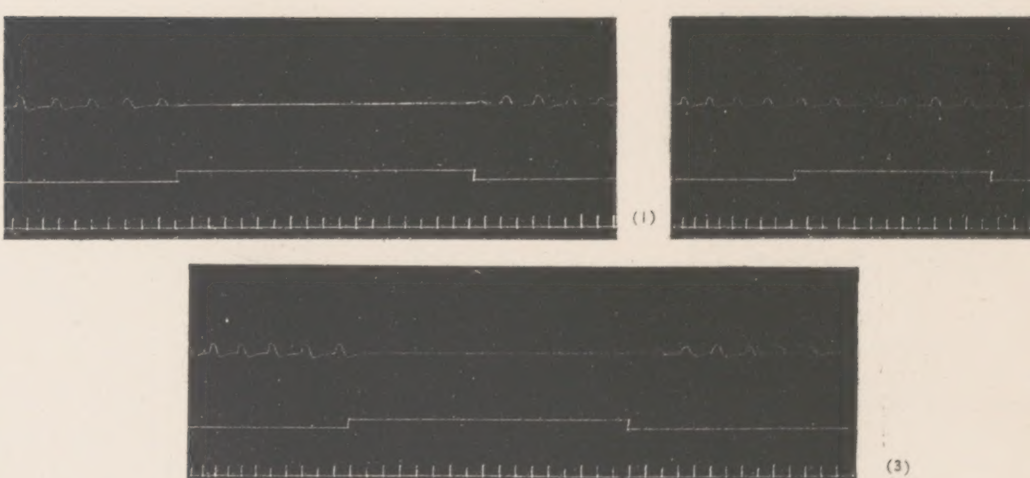

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Fig. III.

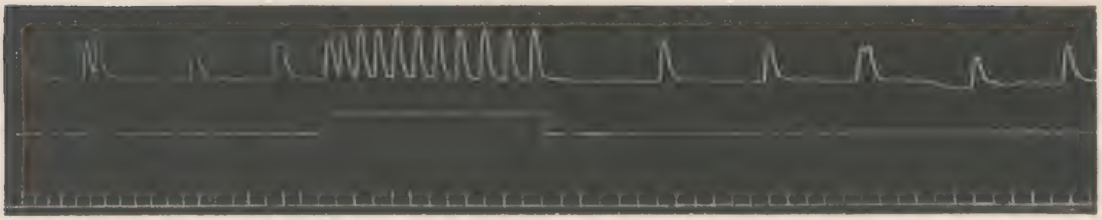

Fig. IV.

Fig. V.

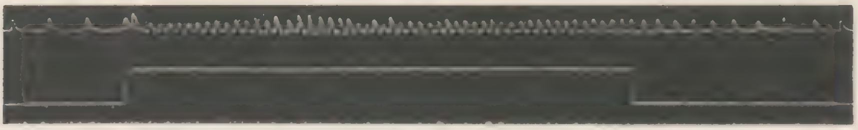

Fig. VI.

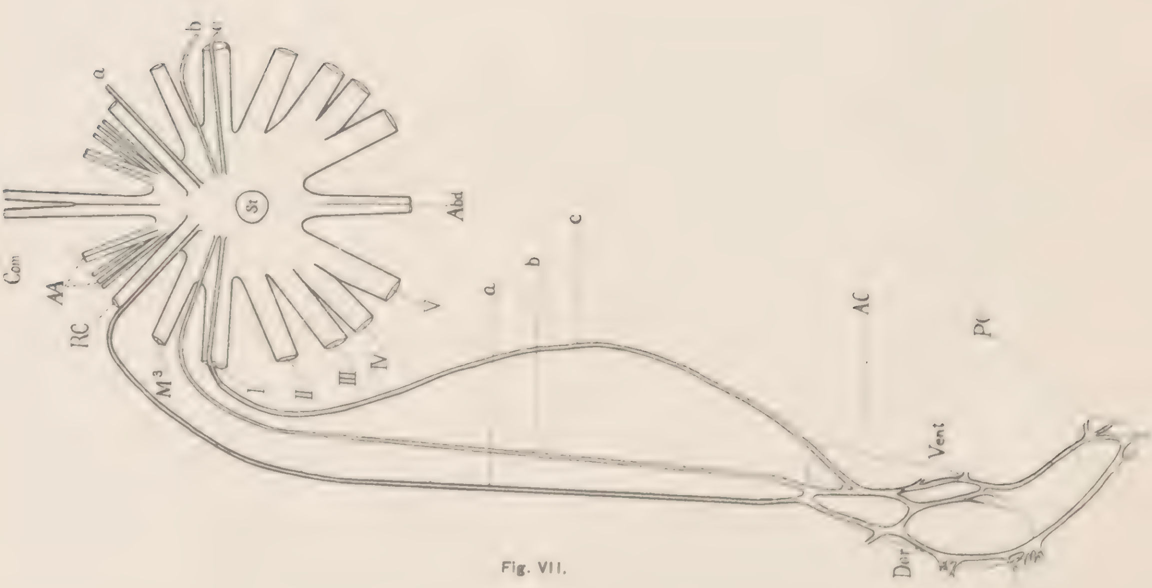

Fig. VII.

any effect on the action of the inhibitory or accelerator nerves, showing that at least the main course of the fibres from the plexus to the heart lies anteriorly.

Explanation of the Plates.

Plate XII.

Fig. 1.—(1) Reflex inhibition from stimulation of cerebral ganglion. (2) Cerebral ganglion stimulated after cutting the commissures to the thoracic ganglion. (The tracing to be read from left to right, as all the following. Time record in seconds.)

Fig. 2.—(1) Stimulation of nerve *a* near plexus. (2) The same from another crab, to show the complete inhibition and the improved beat following that were the usual results.

Fig. 3.—(1) Stimulation of thoracic ganglion. (2) The same after cutting the recurrent cutaneous nerves. (3) Stimulation of peripheral end of one of the recurrent cutaneous nerves.

Plate XIII.

Fig. 4.—Stimulation of nerve *c* near plexus.

Fig. 5.—Stimulation of nerve *b* near plexus.

Fig. 6.—Stimulation of peripheral end of one of the first ambulatory nerves, cut near the ganglion.

Fig. 7.—

Thoracic ganglion and left pericardial plexus of *Callinectes hastatus* (3 ×). The ganglion is drawn from the dorsal side. The plexus is laid over on its left side; in its natural position it lies in a plane at right angles to that of the ganglion. Com, œsophageal commissures, passing to cerebral ganglion; AA, nerves to the anterior appendages; RC, recurrent cutaneous nerves; M^3, to the third maxilliped; I, II, III, IV, and V, nerves to the legs; Abd, to the abdomen; St, sternal artery; *a*, inhibitory; *b* and *c*, accelerator nerves; AO, anterior branchio-cardiac orifice; PO, posterior branchio-cardiac orifice; Dor, dorsal; Vent, ventral regions of the plexus.